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Effects of timber harvest on epigeous fungal fruiting patterns and community structure in a northern hardwood ecosystem

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Abstract: Epigeous fungal fruiting has important impacts on fungal reproduction and ecosystem function. Forest disturbances, such as timber harvest, impact moisture, host availability, and substrate availability, which in turn may drive changes in fungal fruiting patterns and community structure. We surveyed mushrooms in 0.4 ha patch cuts (18 months post-harvest) and adjacent intact hardwood forest in northern New Hampshire, USA, to document the effects of timber harvest on summer fruiting richness, biomass, diversity, and community structure of ectomycorrhizal, parasitic, and saprobic mushroom taxa. Fungal fruiting richness, diversity, and community heterogeneity were greater in intact forests than patch cuts. Among functional groups, ectomycorrhizal fruiting richness, diversity, and biomass were greater in unharvested areas than in the patch cuts, but parasitic and saprobic fruiting did not differ statistically between the two forest conditions. Our findings suggest that timber harvest simplifies fungal fruiting communities shortly after harvest, in particular triggering declines in ectomycorrhizal taxa which are important symbionts facilitating tree establishment and regeneration. Multi-aged silvicultural practices that maintain mature forest conditions adjacent to and throughout harvested areas through deliberate retention of overstory trees and downed woody material may promote fungal fruiting diversity in regenerating stands.

Key words: ectomycorrhizal fungi, epigeous sporocarp, fungal fruiting body, forest disturbance, fungal diversity.

Résumé : La fructification des champignons épigés a des répercussions importantes sur la reproduction des champignons et la fonction de l'écosystème. Les perturbations de la forêt, telles que la récolte de bois, ont un impact sur l'humidité ainsi que la disponibilité des hôtes et du substrat, ce qui en retour peut amener des changements dans les patrons de fructification des champignons et la structure de la communauté. Nous avons inventorié les champignons dans des coupes par trouées de 0,4 ha (18 mois après la récolte) et dans des forêts feuillues adjacentes intactes dans le nord du New Hampshire, aux États-Unis, pour documenter les effets de la récolte de bois sur la diversité, la biomasse et la richesse des fructifications durant l'été ainsi que sur la structure de la communauté des taxons de champignons ectomycorhiziens, parasites et saprobies. La richesse et la diversité des fructifications fongiques ainsi que l'hétérogénéité des communautés étaient plus élevées dans les forêts intactes que dans les coupes par trouées. Parmi les groupes fonctionnels, la richesse, la diversité et la biomasse des fructifications des champignons ectomycorhiziens étaient plus élevées dans les zones non récoltées que dans les coupes par trouées. Par contre, dans les deux situations la fructification des champignons parasites ou saprobies n'était pas significativement différente. Nos résultats indiquent que la récolte de bois simplifie les fructifications des communautés fongiques peu de temps après la récolte, surtout en provoquant le déclin des taxons ectomycorhiziens, lesquels sont des symbiotes importants qui facilitent la régénération et l'établissement des arbres. Les pratiques sylvicoles inéquiennes qui maintiennent les conditions de la forêt mature adjacente aux zones récoltées et parmi ces zones par la rétention délibérée d'arbres dominants et de matériel ligneux au sol, peuvent promouvoir la diversité des fructifications fongiques dans les peuplements en régénération. [Traduit par la Rédaction]

Mots-clés : champignons ectomycorhiziens, sporocarpe épigé, fructification fongique, perturbation de la forêt, diversité fongique.

Introduction

Epigeous fungal sporocarps (mushrooms) play a critical role in fungal reproduction (Brown and Casselton 2001) and have secondary impacts on food webs (e.g., Orledge and Reynolds 2005), forest health (Ostry and Laflamme 2008), and nutrient cycling (Clemmensen et al. 2015). The abundance and spatial distribution of mushroom fruiting depend on several factors, including moisture (Sato et al. 2012), temperature (Kauserud et al. 2008), and host or substrate composition (Krah et al. 2018). Forest disturbances, including timber harvest, alter each of these factors. Timber harvest may decrease soil depth and moisture by causing erosion and compaction (Solgi and Najafi 2014), increase soil and substrate temperature by reducing canopy cover (Ballard 2000), and alter host and substrate availability by removing living trees while simultaneously increasing woody material in the form of

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slash. Consequently, timber harvest drives changes in mushroom fruiting patterns (Tomao et al. 2020).

Effects of timber harvest on mushroom fruiting have been examined at the species level, with reports of increased (Bonet et al. 2012) or decreased (Parladé et al. 2017) fruiting post-harvest. An alternate approach is to look more broadly at the responses among ectomycorrhizal, parasitic, or saprobic functional groups (e.g., Fernández-Toirán et al. 2006). For instance, ectomycorrhizal fungi, which are symbionts of many tree species, have been shown to exhibit lower mushroom richness after timber harvest (Durall et al. 2006). Composition of belowground ectomycorrhizal communities also change after timber harvest (Jones et al. 2003), an effect that is magnified at increasing distances from adjacent intact forest (Durall et al. 1999). Removal of host trees may be detrimental to the survival and fruiting of ectomycorrhizal mushrooms as a group, which may in turn decrease the ability of ectomycorrhizal fungi to disperse to new tree seedlings, particularly in large cutblocks (Hagerman et al. 1999). By contrast, mushrooms of saprobes (decay taxa) and parasites (pathotrophic fungi that attack trees, insects, or other fungi) show a mixed response to forest harvest. Some saprobic and parasitic species (perhaps light or temperature-responsive species) increase fruiting abundance in response to canopy openings, whereas other species fruit less (Siitonen et al. 2005). Response may also differ based on host availability for parasitic taxa, or on substrate requirements, such as between humicolous and lignicolous saprobes (Fernández-Toirán et al. 2006). Whereas the humus layer required by humicolous saprobes is often thin in recently harvested forest due to disturbance by harvesting operations, the woody material required by wood-decay (lignicolous) saprobes may be abundant after forest harvest. Certain lignicolous saprobes have been shown to increase fruiting in cleared areas when there is sufficient slash left behind (Ylisirniö et al. 2012), and diversity of this group may increase when different sizes of woody material are available (Brazee et al. 2014). Due to the availability of large amounts of woody material following timber harvest, the speed with which wood-decaying saprobes proliferate has important implications for nutrient cycling and carbon storage.

This study documents patterns of fungal fruiting very early in the process of forest recovery (approximately 18 months post-harvest). The short-term effects of timber harvest on mushroom fruiting patterns and early fungal succession are little-documented, as most studies are conducted at least 4 years post-harvest (e.g., Durall et al. 2006; Brazee et al. 2014), once forest regeneration is well underway. It is important to document fruiting patterns in the years immediately following forest harvest, as these patterns offer insight into both the resilience of previously established taxa to shifting biotic and abiotic conditions, and the ability of existing or newly established taxa to quickly capitalize on freshly available resources. This is especially the case in northern New England, USA, where timber harvest is a common form of disturbance (Kittredge et al. 2003) and is likely to increase due to salvage operations associated with climate change-induced disturbances such as invasive insect outbreaks and increasingly frequent windthrow and ice events (Dale et al. 2001). The vigor of mushroom fruiting in the immediate aftermath of forest disturbance, particularly at the functional scale (ectomycorrhizal, parasitic, saprobic), likely precipitates numerous downstream effects on nutrient cycling, trophic interactions, and the establishment of mycorrhizal mutualisms that impact forest community structure for decades. As such, documenting these early patterns is critical to informing an understanding of the role post-disturbance fungal fruiting has in driving long-term patterns in key forest ecosystem processes and dynamics.

Materials and methods

Study site

Fieldwork was conducted at 10 study plots located at the Second College Grant, a 10 800 ha forested property owned by Dartmouth College, in Coos County, New Hampshire, USA. This is a temperate, mixed forest system subject to warm summers and cool, snowy winters. Mean annual precipitation and temperature in the region are 1179 mm and 3.2 °C, respectively (Petrenko and Friedland 2015). Each plot consisted of a circular, 0.4 ha patch cut surrounded by a lightly harvested forest matrix last thinned between 1996 and 2000 (Jevon et al. 2019). All patch cuts were harvested between August and December 2017, and eight were harvested in association with the Adaptive Silviculture for Climate Change project, an international network of studies testing different approaches to forest adaptation in the face of climate change and shifting disturbance regimes (Nagel et al. 2017). Experimental harvests were created by hand-felling of all overstory stems with the exception of the deliberate retention of three to four legacy trees per patch for ecological and adaptation objectives. Felled trees were delimbed in the forest with tops left on site and merchantable bolewood removed by cable skidders that accessed patches using pre-designated skid trails. Basal area ranged from 25.7–27.0 m^2/ha prior to harvest and canopy trees were approximately 80–90 years old.

All plots were located in northern hardwood stands, ranging from 84% to 100% hardwood by basal area. Dominant canopy species (note: asterisks indicate ectomycorrhizal associates following Brundrett 2009) included sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.*), and yellow birch (*Betula alleghaniensis* Britt.*), with smaller components of red maple (*Acer rubrum* L.), white birch (*Betula papyrifera* Marsh.*), red spruce (*Picea rubens* Sarg.*), quaking aspen (*Populus tremuloides* Michx.*), and bigtooth aspen (*Populus grandidentata* Michx.*). Composition of all unharvested forest was approximately 40% ectomycorrhizal canopy species by basal area, and 60% non-ectomycorrhizal species. Dominant woody understory species included striped maple (*Acer pensylvanicum* L.), hobblebush (*Viburnum lantanoides* Michx.), and American beech saplings. In the harvested areas, regenerating vegetation was dominated by a patchwork of aspen spp. and pin cherry (*Prunus pensylvanica* L.) saplings, red elderberry (*Sambucus racemosa* L.), red raspberry (*Rubus idaeus* L.), common hemp-nettle (*Galeopsis tetrahit* L.), and various grasses (Poaceae). Mean proportional ground cover of woody material was approximately twice as high per unit area in the patch cuts (14.35% ± 0.95%; mean ± standard error of the mean) as it was in the nearby forest (6.78% ± 0.65%).

Mushroom collection and identification

To document differences in summer fruiting patterns between the recent patch cuts and adjacent forest, we surveyed epigeous sporocarps (mushrooms) at each of the 10 plots in both July and August 2019. This was approximately 18 months after harvest which allowed one growing season for fungal communities to adjust to new environmental conditions and for fungal colonization of new woody material to begin. Surveys were conducted along two 60 m (2 m wide) belt transects, for a total of 240 m^2 surveyed per plot each month. Each transect began in the center of the patch cut, extended 30 m to the edge of the cut, and then continued an additional 30 m into the adjacent forest. Transects were located on opposite sides of each cut.

All mushrooms greater than 0.5 cm in width were counted within each belt transect, and substrate and location were recorded. Specimens not identified in the field were assigned to a temporary "morphotype" based on substrate, growth habit, coloration, and other physical characteristics, and later identified in the lab. Each mushroom was photographed in situ and up to three representative specimens per taxon or morphotype were harvested per plot each month. Specimens were dried in a dehydrator within 24 h of collection and stored for later identification and analysis.

In the lab, unknown mushrooms were identified to genus (or species where possible; approximately 70%). Identification was based on a combination of microscopic analysis of morphological features and macroscopic analysis of dried specimens, photographs of fresh specimens, staining, spore print color (when

available), and field notes on growth habit and substrate. A variety of resources were used for specimen identification, including Baroni (2017), Barron (1999), Beug et al. (2014), Kuo (2021), and Lincoff (1981). Approximately 1% of mushrooms, accounting for 0.03% of total surveyed biomass, were not successfully identified to genus and were excluded from analysis.

The mass of all dehydrated mushroom specimens collected during field surveys was recorded. For each plot, the total fruiting biomass of each taxon was calculated by multiplying the mean dry mass of all collected specimens by the number of mushrooms of that taxon detected within the plot. In instances where frequently recurring taxa were not collected from every location on a transect (only three representative specimens were collected per plot), we assigned an estimated biomass value, calculated as the mean dry biomass of all other specimens of that taxon from the same plot and survey.

Mushrooms were also assigned to one of three functional groups based on taxonomy (genus) and substrate: ectomycorrhizal, parasitic, or saprobic. Functional groups were assigned using the FUNGuild database query tool (http://www.funguild.org, accessed 19 November 2020). For any genera listed in this database as including species from multiple functional groups, we assigned the functional group of the specific taxa occurring at our plots. For instance, the genus *Entoloma* contains species reported to belong to all three functional groups, but each of the species we identified as occurring at our study plots (e.g., *Entoloma quadratum*) is believed to be saprobic, so the genus *Entoloma* was treated as saprobic in analyses. Parasitic mushrooms included both true parasites and taxa that may exhibit both parasitic and saprobic function throughout their life cycles, such as the genera *Fomitopsis* and *Ganoderma*. Taxa with poorly understood functionality (e.g., *Hygrocybe*; Lodge et al. 2014) and unidentified morphotypes were not assigned to a functional group. These taxa accounted for approximately 1% of fruiting bodies. Representative voucher specimens were deposited in the fungarium of the Natural History Museum of Utah (Salt Lake City, Utah).

Analysis

To ensure a robust comparison of fruiting patterns in the patch cuts relative to the intact forest, we filtered out edge effects by excluding data recorded within 10 m of the patch cut-forest edge in either direction. July and August data were combined to represent summer fruiting patterns. To avoid double-counting of fruiting bodies between the study periods, conks and other long-lasting fruiting bodies were not counted in the August surveys when they matched the location and description of fruiting bodies observed in the July surveys.

At the genus level, we compared the number of individual fruiting bodies observed in the patch cut to the number observed in the forest using a Wilcoxon signed-rank test [*wilcox.exact*] in the R package "exactRankTests" (Hothorn and Hornik 2019). At the functional group level, we compared fruiting between the patch cut and the forest for all three functional categories using several metrics: genus richness, dry biomass, and Shannon–Wiener diversity index. Biomass was chosen over fruiting abundance at the functional group scale to avoid biasing results in favor of fungal taxa that produced numerous small fruiting bodies over taxa that produced individual, large fruiting bodies. Mean genus richness and mean dry biomass were compared using the Wilcoxon signed-rank test. To evaluate the effect of patch cuts on fungal fruiting composition, we used a Bray–Curtis dissimilarity matrix generated from biomass data for all genera detected at more than one study plot. To visualize trends in compositional similarity among plots we used non-metric multidimensional scaling (NMDS) in the R package "vegan" (Oksanen et al. 2019). One patch cut was excluded from community analyses because it only contained one mushroom taxon detected at other plots. To quantify the role of timber harvest on community composition, we used PERMANOVA (multivariate repeated-measures analysis of variance (ANOVA) – function [*adonis*] in vegan), applying the repeated measures by using 1000 randomized datasets. To test for homogeneity of dispersion between communities in the patch cuts and forests, we used the betadisperser function in vegan. All statistical analyses were conducted in R version 3.6.2 (R Core Team 2019).

Results

We detected over 3,000 mushrooms belonging to at least 63 genera, including 11 ectomycorrhizal genera, 6 parasitic genera, and 42 saprobic genera (Appendix Table A1). Of these taxa, six (10%) were detected only in patch cuts, 38 (60%) were detected only in forests, and 19 (30%) were detected in both forests and patch cuts. Additionally, 40 genera (63%) were detected at only 1 of the 10 study locations. This reflects the diversity and ephemerality of the fruiting body community and suggests that only a fraction of present taxa were detected in our single-year study, a pattern observed elsewhere even over many consecutive years of study (Straatsma et al. 2001). Likely due to small sample sizes, only three genera were found to fruit significantly more in either the patch cuts or the forests. Fruiting bodies of the genus *Schizophyllum* were more abundant in the patch cuts ($z = -2.93$, $p = 0.008$), and the genera *Hygrocybe* ($z = -2.48$, $p = 0.040$) and *Entoloma* ($z = -2.49$, $p = 0.040$) fruited more abundantly in the forests.

At the functional group level, several differences in mushroom fruiting were observed between the patch cuts and forests. Mean fruiting richness of all genera combined, including those not assigned to a functional group, was greater in the forests than in the patch cuts ($z = -2.35$, $p = 0.010$; Fig. 1). Mean richness was also greater in the forest for fruiting bodies of ectomycorrhizal taxa specifically ($z = -2.36$, $p = 0.024$), and ectomycorrhizal fruiting body biomass in the forest was approximately 10 times greater than in the patch cuts ($z = -2.15$, $p = 0.043$). In contrast, saprobic and parasitic fruiting body richness and biomass did not vary significantly between the patch cuts and forests. Fruiting biomass for all functional groups combined also did not differ. Shannon–Wiener diversity values were higher in the forest than in the patch cut, both for all taxa combined and for each individual functional category.

PERMANOVA indicated that fungal fruiting body community composition was significantly different between patch cuts and the forest ($F_{[1,19]} = 1.65$, adjusted $p = 0.042$). The degree of fruiting community concordance was also significantly greater in patch cuts than in forests ($p = 0.014$). These relationships were apparent in the NMDS ordination (based on 25 genera that occurred at two or more plots), with slight separation between the two groups of communities along the horizontal axis, and a notably smaller ellipse spread around the centroid for fungal communities in patch cuts (Fig. 2).

Discussion

Forest harvest resulted in lower overall mushroom richness and diversity 18 months post-harvest. Although approximately one third of genera were present in both patch cuts and surrounding forests, results from our betadisperser test and NMDS ordination indicate that there was less heterogeneity in fungal communities associated with harvested areas relative to intact forest communities. This greater community homogeneity is suggestive of structural simplification of the fungal community after harvest driven by the loss of many ectomycorrhizal and saprobic taxa, a pattern previously observed in a number of other regions (Tomao et al. 2020). Shifts in community concordance may also be attributable to abundant fruiting of early decay taxa colonizing slash in the patch cuts.

Indeed, a number of wood-decaying saprobic taxa were particularly abundant on slash in the patch cuts. One such taxon, *Schizophyllum*, was represented entirely by the species *S. commune*, and

Fig. 1. Values (means ± standard error of the mean) for genus richness, Shannon–Wiener diversity index (also at the genus level), and dry biomass of fruiting bodies per survey for all functional groups combined and for ectomycorrhizal (ECM), parasitic, and saprobic groups individually. Asterisks indicate significance ($p < 0.05$). Note that y axes are scaled independently.

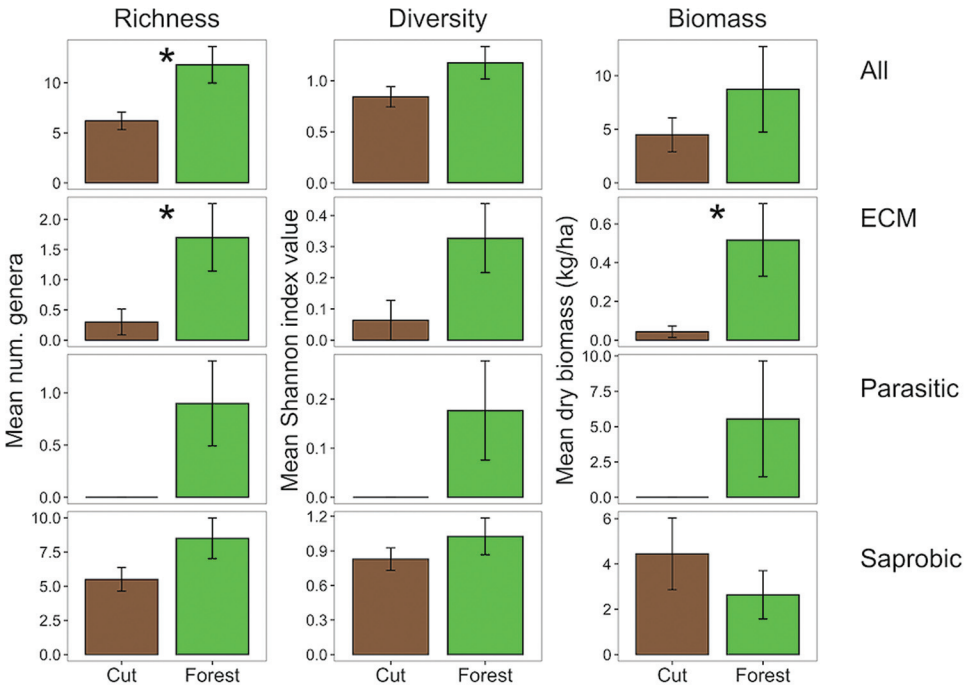
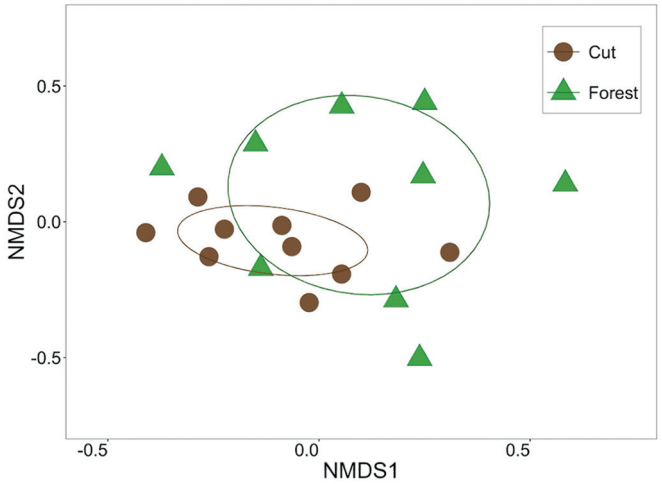


Fig. 2. Two-dimensional nonmetric multidimensional scaling (NMDS) ordination (final stress = 0.15) of mushroom communities in patch cuts (circles, $n = 10$) and forests (triangles, $n = 9$). Greater pairwise distance between markers indicates decreased similarity in community composition. Ellipses represent 50% confidence intervals around the centroid, and ellipse size approximates relative community concordance.



was the most commonly detected taxon in this study (Table A1). On average, fruiting bodies of *S. commune* were over seven times more abundant in the patch cuts than in the forest. Fruiting of this species may be enhanced by high density of slash, as there was approximately twice as much woody cover in the patch cuts as there was in the forests. Other taxa that were abundant on fresh slash included several species of the genus *Trametes*, as well as the genera *Irpex* (represented entirely by *Irpex lacteus*) and *Trichaptum* (represented by *Trichaptum biforme*), although none of these were statistically more abundant in the patch cuts than in the intact forest. Our findings are similar to those of a study in the midwestern United States, which reported no difference in abundance of *T. biforme* and *I. lacteus* between small gap cuts and forest habitat, although significantly higher abundance of three different species of *Trametes* was detected in the cuts (Brazee et al. 2014). Differences in quantity, size class, and decay stage of available deadwood in harvested areas may impact the degree and rapidity with which these early decay saprobes fruit in recent cuts.

Fruiting patterns observed in saprobes may also depend on how recently timber harvests occurred. Slightly older cuts (up to 10 years post-harvest) with abundant saplings are reported to contain higher species richness of wood-inhabiting fungi than any later successional stage (Junninen et al. 2006). This may be caused by a greater diversity of woody material size and decay class, due to a combination of fresh woody material from harvest activity and existing woody material remaining from the pre-harvest period. Although our study did not analyze wood-inhabiting fungi as a group separately from other saprobic taxa, our analyses of saprobic and parasitic fungi overall do not suggest that patch cuts 18 months post-harvest are particularly taxonomically diverse. This discrepancy in findings may be caused by a combination of factors, including the differing stages of succession between the two studies. Greater time since harvest may result in greater sapling coverage and canopy cover which may result in woody substrates with higher moisture content, generally assumed to correlate positively with fungal fruiting. Additionally, the younger age of deadwood in our study (slash was <2 years old, as opposed to <10 years old) may limit saprobe richness, as older deadwood appears to decay heterogeneously and play host to a greater variety of wood-inhabiting species than fresh deadwood (Tomao et al. 2020). If young patch cuts do indeed provide habitat for only a limited suite of common saprobes, taxonomic richness and habitat for uncommon species may be improved by efforts that retain or minimize disturbance to key biological legacies contributing to saprobe

diversity. This may include leaving patches of understory shrubs and advance regeneration, a variety of woody material size and age classes (Brazee et al. 2014), or even whole dead trees (Heilmann-Clausen and Christensen 2004), during harvest.

Parasitic fungi, including both polyporoid conk fungi that often parasites living trees (e.g., *Ganoderma*) and parasites of fungi (e.g., *Tremella*) and insects (e.g., *Cordyceps*), were frequently detected in the forests but were entirely absent from the patch cuts. This is likely because hosts were removed or displaced during timber harvest. The removal of large-diameter host trees and any overall decrease in large-diameter deadwood (another important substrate for many polypores; Toivanen et al. 2012), should decrease the fruiting of parasitic polypores, by far the most abundant class of parasites detected in our surveys. Timber harvest may also impact the availability of hosts for non-polyporoid parasites. For instance, the saprobic genus *Stereum*, host to the parasitic fungus *Tremella aurantia*, was found almost exclusively in intact forest (Table A1). Similarly, forest harvest typically disrupts communities of moths and butterflies (Summerville and Crist 2002), important hosts of the parasite *Coryceps militaris* (Shrestha et al. 2016). Taken together, logging-induced declines in various host taxa would likely decrease the fruiting of parasitic mushrooms as a group. Yet, parasitic fungi were so highly variable in abundance, often due to dense clusters of conk fungi on individual trees, that no statistical difference in biomass or richness was detected between patch cuts and forests.

Ectomycorrhizal fruiting decreased sharply in response to timber harvest, with declines evident in richness and diversity of genera along with mean biomass of fruiting bodies. Similar trends have been documented in western North America, suggesting that forest harvest consistently decreases the fruiting of ectomycorrhizal mushrooms as a group (Durall et al. 2006). While this decrease in fruiting is not necessarily indicative of a similar loss of ectomycorrhizal taxa belowground (Gardes and Bruns 1996), several studies suggest that timber harvest alters belowground ectomycorrhizal communities as well (Byrd et al. 2000; Jones et al. 2003; Parladé et al. 2019). Shifts in ectomycorrhizal communities and fruiting patterns may be driven by increased soil temperatures, decreased moisture availability due to harvest disturbance of the forest floor, or otherwise inhospitable environmental conditions post-harvest, in addition to the direct losses of host trees. Perhaps importantly, much of the regenerating woody vegetation in the patch cuts was dominated by non-ectomycorrhizal plant species, such as red elderberry and pin cherry. Dominance of these non-ectomycorrhizal species could conceivably reduce abundance of ectomycorrhizal fungal taxa in the immediate aftermath of timber harvest. Root tip colonization of new seedlings steadily decreases at increasing distances from living trees, with the lowest colonization rates occurring beyond 15 m from live trees (Dickie and Reich 2005). Moreover, ectomycorrhizal fruiting richness is reported to decrease exponentially with increasing cutblock size (Durall 1999), an effect that can be partially offset by the retention of mature trees in harvested areas (Luoma et al. 2004). This suggests that intact forests, as well as mature retention trees, play an important role in maintaining ectomycorrhizal communities belowground, which (coupled with other environmental variables) would help to explain the marked difference in ectomycorrhizal mushroom fruiting that we observed between patch cuts and nearby forest.

It is worth noting that some ectomycorrhizal taxa are sensitive even to low-intensity timber harvest regimes (Leski et al. 2019). These sensitive taxa may not be represented in our surveys due to the history of light thinning in the intact forest. Nevertheless, the absence of additional ectomycorrhizal taxa in the forest stands is unlikely to have biased our comparison of fruiting between patch cuts and intact forest.

Timber harvest may reduce opportunities for direct and indirect ectomycorrhizal spore dispersal to potential seedling symbionts. For instance, declines in mushroom fruiting caused by timber harvest likely decrease the quantity of spores dispersed locally by wind. Many ectomycorrhizal taxa also rely on fungivorous mammal and invertebrate species for indirect dispersal (Halbwachs and Bässler 2015), including several small mammal species known to consume and disperse large quantities of ectomycorrhizal mushrooms in this region (Stephens and Rowe 2020). Harvest-induced changes in canopy and ground cover coupled with declines in fruiting likely alter habitat suitability or movement patterns of these dispersers and thus reduce spore dispersal. Dietary shifts in small mammals and invertebrates driven by declines in ectomycorrhizal mushrooms may also have cascading impacts on forest food web structure and function.

Our functional group findings are likely representative of broader trends beyond the 1 year of sampling. Fruiting of individual ephemeral species is often inconsistent and difficult to predict in any given year (Straatsma et al. 2001); however, interannual fruiting patterns are more predictable by functional type. Mycorrhizal and saprobic mushroom fruiting abundance appear to fluctuate in concert from year to year (Straatsma and Krisai-Greilhuber 2003), even while exhibiting high variability at the species level and years of high and low fruiting overall. The vast majority of parasitic and many saprobic taxa documented in this study form fruiting bodies over the course of several years, so it is unlikely that patch cut-forest differences in fruiting abundance in these functional groups would vary greatly from year to year. Taking all of this into account, we suggest that the fruiting patterns we observed at the functional level are broadly representative of differences in epigeous fungal fruiting between patch cuts and intact forests in the years immediately following harvest. If relative differences in fruiting abundance at the functional level between patch cut and forest shifted among years, this would likely be indicative of directional change in fungal fruiting communities (succession) rather than interannual fluctuation in fruiting patterns. Furthermore, limiting sampling to summer months is unlikely to have biased the trends detected in this study. While it is plausible that seasonal differences in moisture and temperature could result in fruiting differences in patch cuts relative to forests, other studies that have sampled during a broader temporal window including both the spring and fall seasons (e.g., Durall et al. 2006) have documented similar trends to those observed here. Continued monitoring of these cuts over the coming years would confirm whether long-term trends mirror those of immediate response windows.

We demonstrate that timber harvest led to stark differences in fungal fruiting patterns in the second summer following harvest. These differences were particularly evident at the community level, with lower richness and diversity, as well as greater community concordance, in the patch cuts than in the surrounding forest. Among functional groups, ectomycorrhizal fungi were most impacted by timber harvest with decreased fruiting richness, biomass, and diversity in the patch cuts. Changes in fungal fruiting abundance and community structure at this early point following timber harvest have downstream implications for fungal population connectivity, ecosystem health, nutrient cycling, and forest regeneration. In northern New England, where large parcels are commonly managed for timber production (Daigle et al. 2012), silvicultural strategies that incorporate impacts on fungal taxa may in turn enhance forest regeneration by supporting the ectomycorrhizal fungal communities critical for nutrient acquisition by trees. Strategies of particular interest may include retention of downed woody material and live overstory and understory trees, particularly ectomycorrhizal tree species such as *Betula* spp., as well as strategies that prioritize recolonization of harvested areas specifically by ectomycorrhizal tree seedlings. Such practices, aimed at maintaining mature forest conditions adjacent to and throughout harvested areas, may preserve mycorrhizal communities and soil conditions requisite for fungal fruiting, thereby promoting more diverse fungal fruiting communities.

Author contributions

Conceptualization: BBW, RBS, RJR; Investigation: BBW, RBS; Methodology and Formal Analysis: BBW, RBS; Writing – Original Draft: BBW; Writing – Review & Editing: RBS, RJR, SDF, AWD; Resources: AWD, SDF, RJR; Funding Acquisition: RBS, AWD, SDF, RJR.

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Appendix Table A1 appears on the next page.

Appendix A

Table A1. Observed fruiting bodies and abundance by genus (organized by functional type).

Genus	No. of plots detected ($n = 10$)	Total found in forest	Total found in cut	Functional group
Amanita	3	2	3	Ectomycorrhizal
Boletus	2	2	0	Ectomycorrhizal
Clavulina	1	49	0	Ectomycorrhizal
Clavulinopsis	2	5	0	Ectomycorrhizal
Cortinarius	1	1	0	Ectomycorrhizal
Inocybe	2	3	0	Ectomycorrhizal
Leccinum	1	1	0	Ectomycorrhizal
Russula	4	3	2	Ectomycorrhizal
Scleroderma	1	4	0	Ectomycorrhizal
Suillus	2	2	0	Ectomycorrhizal
Tricholoma	1	1	0	Ectomycorrhizal
Cordyceps	1	1	0	Parasitic
Fomes	2	38	0	Parasitic
Fomitopsis	2	8	0	Parasitic
Ganoderma	2	4	0	Parasitic
Phellinus	1	1	0	Parasitic
Tremella	1	7	0	Parasitic
Agrocybe	1	2	0	Saprobic
Apioperdon	1	1	0	Saprobic
Bisporella	3	10	1	Saprobic
Calocera	1	18	0	Saprobic
Camarops	1	0	5	Saprobic
Cerioporus	3	5	1	Saprobic
Clitocybe	1	5	0	Saprobic
Collybia	1	1	0	Saprobic
Crepidotus	2	8	1	Saprobic
Cudonia	1	1	0	Saprobic
Dacrymyces	1	7	0	Saprobic
Daedaleopsis	1	0	4	Saprobic
Entoloma	3	17	0	Saprobic
Galerina	1	1	0	Saprobic
Gymnopilus	1	0	2	Saprobic
Gymnopus	2	4	0	Saprobic
Hymenochaete	2	53	0	Saprobic
Hypoxylon	2	252	0	Saprobic
Inocephalus	1	0	2	Saprobic
Irpex	4	3	59	Saprobic
Marasmiellus	1	2	0	Saprobic
Marasmius	7	34	173	Saprobic
Megacollybia	5	13	1	Saprobic
Mycena	6	12	24	Saprobic
Neobulgaria	1	22	0	Saprobic
Neofavolus	1	3	0	Saprobic
Panellus	1	20	0	Saprobic
Peziza	3	2	3	Saprobic
Phlebia	2	2	0	Saprobic
Plicaturopsis	2	303	32	Saprobic
Pluteus	5	3	3	Saprobic
Psilocybe	6	13	8	Saprobic
Pycnoporus	4	0	18	Saprobic
Schizophyllum	9	100	1110	Saprobic
Scutellinia	4	18	13	Saprobic
Steccherinum	1	20	0	Saprobic
Stereum	4	322	6	Saprobic
Tatraea	1	1	0	Saprobic
Trametes	9	274	556	Saprobic
Trichaptum	3	28	196	Saprobic
Tyromyces	4	27	10	Saprobic
Xylaria	2	2	0	Saprobic
Gliophorus	1	3	0	Unknown
Helvella	1	1	0	Unknown
Hygrocybe	5	20	0	Unknown
Rickenella	1	0	7	Unknown

Note: Nomenclature based on Index Fungorum taxonomy (http://www.IndexFungorum.org, accessed 5 Nov. 2020). The genus *Clavulinopsis* was categorized as ectomycorrhizal following Birkebak et al. (2013). Note that many taxa were detected in only one stand (i.e., plot).